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Abstract. Foundation species are basal species that play an important role in determining community composition by physically structuring ecosystems and modulating ecosystem processes. Foundation species largely operate via non-trophic interactions, presenting a challenge to incorporating them into food-web models. Here, we used non-linear, bioenergetic predator-prey models to explore the role of foundation species and their non-trophic effects. We explored four types of models in which the foundation species reduced the metabolic rates of species in a specific trophic position. We examined the outcomes of each of these models for six metabolic rate "treatments" in which the foundation species altered the metabolic rates of associated species by one-tenth to ten times their allometric baseline metabolic rates. For each model simulation, we looked at how foundation species influenced food-web structure during community assembly and the subsequent change in food-web structure when the foundation species was removed. When a foundation species lowered the metabolic rate of only basal species, the resultant webs were complex, species-rich, and robust to foundation species removals. On the other hand, when a foundation species lowered the metabolic rate of only consumer species, all species, or no species, the resultant webs were species-poor and the subsequent removal of the foundation species resulted in the further loss of species and complexity. This suggests that in nature we should look for foundation species to predominantly facilitate basal species.

Key words: foundation species, food-web modeling, metabolic rate, network, non-linear dynamics

INTRODUCTION

Foundation species (sensu Dayton 1972) are basal species that structure ecological communities by creating physical structure and modulating ecosystem processes (Ellison et al. 2005). Recent declines (e.g., *Tsuga canadensis*) and extirpations (e.g., *Castanea dentata*) of foundation species in terrestrial ecosystems have called attention to the need for new methods for identifying and quantifying the role of foundation species in ecological communities (reviewed by Ellison et al. 2005; 2010, Van der Putten 2012). Numerous field studies have shown that foundation species can alter trajectories of the assembly of ecological communities (e.g., Gibson et al. 2012, Schoeb et al. 2012, Butterfield et al. 2013, Martin and Charles 2013, Orwig et al. 2013). However, general models of how foundation species affect ecological systems are scarce and generally qualitative (Ellison and Baiser, *in press*).

Foundation species can interact trophically within a community, but they exert their influence primarily through non-trophic effects (Ellison and Baiser, *in press*). Some examples of non-trophic actions of foundation species include; altering local climates and microclimates (e.g., Schoeb et al. 2012, Butterfield et al. 2013); changing soil temperature, moisture, and acidity (e.g., Prevey et al. 2010, Lustenhouwer et al. 2012, Martin and Charles 2013); providing refuge for prey species and perches for predators (e.g., Yakovis et al. 2008, Tovar-Sanchez et al. 2013) ; and stabilizing stream banks and shorelines against erosion (reviewed by Ellison et al. 2005). Because foundation species exert system-wide effects on biodiversity and ecosystem functioning primarily through these (and other) non-trophic interactions, it has proven difficult to link effects of foundation species into theories of the structure and function of food webs. Food-web theory aims to elucidate the persistence of the types of complex, species-rich webs that we see in nature (e.g., May 1972, Allesina and Tang 2012). Measures of network properties, such as connectance,

55 compartmentalization, and species richness, as well as the strength of species interactions, all can
56 influence the stability and persistence of food webs (e.g., May 1972, Dunne et al. 2002, Gravel et
57 al. 2011, Stouffer and Bascompte 2011). Adding non-trophic interactions, such as those
58 exhibited by foundation species or mutualists in general, provides an additional step towards
59 understanding persistence and stability of ecological networks (Thébault and Fontaine 2010,
60 Allesina and Tang 2012, Kéfi et al. 2012)

61 Here, we adapt non-linear, bioenergetic predator-prey models to explore non-trophic
62 roles of foundation species in food webs. To make explicit linkages between trophic and non-
63 trophic interactions, we model the metabolic rate of individual "species" as a function of
64 foundation species biomass. Metabolic rate is good proxy for a wide variety of positive non-
65 trophic species interactions (sensu Kéfi et al. 2012), because "stressful conditions" may be
66 reduced when foundation species ameliorate temperature extremes, provide associated species
67 with habitat resources or shelters, or enhance their growth rate (Schiel 2006, Shelton 2010,
68 Gedan et al. 2011, Angelini and Silliman 2012, Dijkstra et al. 2012, Noumi et al. 2012,
69 Butterfield et al. 2013).

70 We developed four different foundation species models to explore non-trophic effects of
71 foundation species in food webs. In each, the foundation species influences target species at
72 different trophic positions in the food web: 1) a *basal model,* in which the foundation species
73 reduces the metabolic rates of only other, albeit non-foundation, basal species, 2) a *consumer*
74 *model,* in which the foundation species reduces the metabolic rates of only consumers, 3) a *total*
75 *model,* in which the foundation species reduces the metabolic rates of all species, and 4) a
76 *control model,* in which the foundation species is only consumed and has no effect on the
77 metabolic rates of any associated species. We examined the outcomes of each of these models

for six metabolic rate "treatments" in which the foundation species alters the metabolic rates of associated species by one-tenth to ten times their allometric baseline metabolic rates. For each model simulation, we looked at how foundation species influence different measures of food-web structure during community assembly and the subsequent change of food-web structure when the foundation species was removed.

METHODS

We modeled dynamic ecological networks using a four-step process (Brose et al. 2006, Berlow et al. 2009, Kéfi et al. 2012): 1) model initial network structure; 2) calculate body mass for each species based on trophic level; 3) simulate population dynamics using an allometric predator-prey model; and 4) add non-trophic interactions into the allometric predator-prey model.

Network structure

We used the niche model of Williams and Martinez (2000) to designate trophic links in our model food webs. The niche model is an algorithm with two parameter inputs: species richness (S) and connectance ($C = L/S^2$, where L = the number of trophic links). Each species in the web has a niche value uniformly drawn from [0,1] and a niche range that is placed on a one-dimensional axis. Any one species whose niche value falls within the niche range of another is defined to be the latter's prey (for specific details on the niche model see Williams and Martinez 2000). The niche model has been shown to reproduce accurately a wide range of food-web network properties for many empirical webs (Williams and Martinez 2000, Dunne et al. 2004, Williams and Martinez 2008).

101

102 *Body mass*

103 We calculated body mass, M_i, for species *i* as:

104

105 $$M_i = Z^{T-1} \qquad (1)$$

106

107 In eq. (1), *Z* is the predator-prey biomass ratio and *T* is the average trophic level of species *i*
108 calculated using the prey-averaged method (Williams and Martinez 2004). We set basal species
109 *M* to unity and used a predator-prey biomass ratio of $Z = 10^2$. We used body mass to
110 allometrically scale biological parameters in the predator-prey model.

111

112 *Allometric predator–prey model*

113 We simulated food-web population dynamics using an allometric predator-prey model
114 (Yodzis and Innes 1992, Williams and Martinez 2004, Brose et al. 2006). Following Brose et al.
115 (2006):

116 $$\frac{dB_i}{dt} = r_i\left(M_i\right)G_iB_i - x_i\left(M_i\right)B_i - \sum_{j=consumers}\frac{x_j\left(M_j\right)y_jB_jF_{ji}\left(B\right)}{e_{ji}f_{ji}} \qquad (2a)$$

117 $$\frac{dB_i}{dt} = -x_i\left(M_i\right)B_i + \sum_{j=resources} x_i\left(M_i\right)y_iB_iF_{ij}\left(B\right) - \sum_{j=consumers}\frac{x_j\left(M_j\right)y_jB_jF_{ji}\left(B\right)}{e_{ji}f_{ji}} \qquad (2b)$$

118

119 Equation 2a describes change in biomass, *B*, of primary producer species *i*, and equation 2b
120 describes changes in *B* of consumer *i*. All model variables are listed and defined in Table 1.

For primary producer species i, r_i is its mass-specific maximum growth rate; M_i is its individual body mass; and G_i is its logistic growth rate: $G_i = 1-(B_i/K)$ and K is the carrying capacity (in our model, $K = 1$). Both for primary producers and consumers, the mass-specific metabolic rate for species i is x_i. For consumers, y_i is the maximum consumption rate of species i relative to its metabolic rate; e_{ji} is the assimilation efficiency for species i when consuming species j; and f_{ij} is the fraction of biomass removed from the resource biomass that is actually ingested. The functional response, F_{ij}, describes how consumption rate varies as a function of prey biomass. We used a type II functional response:

$$F_{ij} = \frac{w_{ij} B_j}{B_0 + \sum_{k=resources} w_{ik} B_k} \qquad (3)$$

In eq. (3), ω_{ij} is the uniform relative consumption rate of consumer i preying on resource j (i.e., the preference of consumer i for resource j) when the consumer has n total resources ($\omega_{ij} = 1/n$) and B_0 is the half-saturation constant (i.e., resource biomass at which consumer reaches half of its maximum consumption rate). In all of our models, B_0 was set equal to 0.5.

Body size is an important component of both predator-prey interactions (Warren and Lawton 1987, Woodward and Hildrew 2002, Brose et al. 2006) and metabolic functioning of organisms (Brown et al. 2004). As a result, body size is an important factor for energy flow throughout food webs (Woodward et al. 2005). Predator-prey body-size ratios found in empirical food webs have been shown to stabilize dynamics in complex networks (Brose et al. 2006). Thus, we allometrically scaled the biological parameters r_i, x_i, and y_i in eqns (2a) and (2b) to body size (Brose et al 2006). We modeled the biological rates of production, R, metabolism, X, and maximum consumption rate, Y, using a negative-quarter power-law dependence on body size (Brown et al. 2004):

143 $$R_P = a_r M_P^{-0.25} \qquad (4a)$$

144

145 $$X_C = a_x M_C^{-0.25} \qquad (4b)$$

146

147 $$Y_C = a_y M_C^{-0.25} \qquad (4c)$$

148 In eqns (4a-4c), subscripts *P* and *C* correspond to producers and consumers respectively; a_r, a_x,
149 and a_y are allometric constants; and *M* is the body mass of an individual (Yodzis and Innes
150 1992). The time scale of the system is specified by fixing the mass-specific growth rate, r_i, to
151 unity. Following this, we normalized the mass-specific metabolic rate, x_i, for all species in the
152 model by time scale and in turn, we normalized the maximum consumption rate, y_i, by the
153 metabolic rates:

154 $$r_i = 1 \qquad (5a)$$

155 $$x_i = \frac{X_C}{R_P} = \frac{ax}{ar}\left(\frac{M_C}{M_P}\right)^{-0.25} \qquad (5b)$$

156 $$y_i = \frac{Y_C}{X_C} = \frac{a_y}{a_x} \qquad (5c)$$

157 We then entered the allometrically scaled parameters for r_i, x_i, and y_i into equations 2a and 2b,
158 yielding an allometrically scaled, dynamic predator-prey model. We set the allometric constants
159 to be $y_i = 8$, $e_{ij} = 0.85$ for carnivores and $e_{ij} = 0.45$ for herbivores, $a_r = 1$, and $a_x = 0.314$ (Yodzis
160 and Innes 1992, Brown et al. 2004, Brose et al. 2006).

161

162 *Foundation species and non-trophic interactions*

163 For each food web, we randomly designated one basal species as a foundation species.
164 Each foundation species engaged in a non-trophic interaction with a given number of target
165 species in a food web, depending on the model described in the next section. The foundation
166 species alters the metabolic rate (x) of a target species with which it interacts following a general
167 saturating function (after Otto and Day 2007):

168 $$\frac{dx_i}{dB} = \frac{x_{fsp}B + x_a B_a}{B + B_a} \qquad (6)$$

169 In eq. (6), x_{fsp} is the metabolic rate of the target species in the presence of the foundation species;
170 x_a is the metabolic rate of the target species in the absence of the foundation species (i.e.,
171 baseline metabolic rate, eqn 5b); B is the biomass density of the foundation species; and B_a is the
172 "typical" (i.e., ~average across trial runs) biomass density for the foundation species. The
173 metabolic rate of species i, x_i, decreases from x_a when $B = 0$ to an asymptote at x_{fsp} when B is
174 large (we assume that $x_{fsp} < x_a$ because the foundation species reduces the metabolic rates of its
175 associated species).
176
177 *Four foundation species models*
178 We varied the number and position of non-trophic interactions in four different ways
179 (Fig. 1). In the *control* model, there are no non-trophic interactions (i.e., the species designated
180 as the foundation species has only trophic interactions). In the *basal model*, the foundation
181 species influences the metabolic rate of all basal species. In the *consumer model*, the foundation
182 species influences the metabolic rate of all consumers (i.e., non-basal species). Finally, in the
183 *total model*, the foundation species influences the metabolic rate of all species in the food web.
184
185 *Simulations and analysis*

We created 100 niche-model webs, in all of which we set $S = 30$ and $C = 0.15$. We parameterized allometric predator-prey models with an initial biomass (B_i) vector drawn randomly from a uniform distribution: $B_i \sim$ Uniform[0.5,1]. The initial value of B_i was the same for any given food web in all four of the foundation species models. We solved equations 2a and 2b using the standard 4^{th} order Runge-Kutta method with a time step of 0.001. For each model run, we ran the initial "food-web assembly" simulations for 2,000 time steps. A species was considered extinct and removed from model simulations (i.e., $B_i = 0$) when $B_i < 10^{-30}$ (Brose et al. 2006, Berlow et al. 2009). At the end of this "assembly" period we calculated the number of species present and nine additional measures of food-web structure (Table 2) and then removed food webs with unconnected species or chains from further simulation. We next "removed" the foundation species from the remaining webs and ran the "foundation species removal" simulation for an additional 2,000 time-steps. At t =4,000, we again calculated the number of species present and the nine additional measures of food web structure (Table 2).

Food-web metrics (Table 2) were calculated using Network 3D (Williams 2010). For the *food web assembly analysis* (i.e., the first 2,000 time steps of each model run), we tested the effect of each model (foundation species effects) using analysis of covariance (ANCOVA). In the ANCOVA, foundation species model was the factor, and log (metabolic rate +1) was the covariate. Because measures of food-web structure are often correlated (Vermaat et al. 2009), we used principle components analysis (prcomp in R version 2.13.1) to reduce the food-web metrics into two orthogonal principle components that were used as response variables in the ANCOVA. In this analysis, we did not include food webs that collapsed (i.e., had zero species). ANCOVA was implemented using glm in R; a Poisson link function was used when species richness was

208 the response variable, and a Gaussian link function was used for the analysis of food-web metrics
209 (principal axis scores).

210 For the *foundation species removal analyses* (i.e., time steps 2,001 – 4,000), we
211 calculated standardized change ($\Delta z = z_{t=2001}\text{-}z_{t=4000} / z_{t=2001}$) in species richness and food-web
212 metrics (principal axis scores) between the end of food-web assembly (t = 2,001) and the end of
213 the foundation species removal (t = 4,000) because webs had different species richness at the
214 time the foundations species was removed (t = 2,000). As described above, we then used
215 ANCOVA to test the effects of each model.

216

217 *Exploring the parameter space*

218 An important assumption in our models is that species have higher metabolic rates in the
219 absence of the foundation species. However, it was not clear how to set the baseline metabolic
220 rate, x_a, (i.e., how poorly should any particular species perform in the absence of the foundation
221 species) and how much the foundation species should improve [= reduce] the metabolic rate
222 (x_{fsp}). To explore a range of reasonable possibilities, we ran one set of simulations in which x_a
223 was set equal to the allometrically scaled metabolic rate in eqn. (5b) and x_{fsp} was set equal to one
224 of 0.5, 0.2 or, 0.1 of x_a (Fig. 2A; referred to henceforth as *0.5*×, *0.2*×, and *0.1*× treatments). In
225 this first set of simulations, species start at the (allometric) baseline and the presence of the
226 foundation species further reduces the metabolic rates of species associated with it. In the second
227 set of simulations, x_{fsp} was set equal to the allometrically scaled metabolic rate in eqn. (5b) and x_a
228 was set equal to one of 2, 5, or 10 times x_{fsp} (Fig. 2B; referred to henceforth as *2*×, *5*×, and *10*×
229 treatments). Our metabolic rates encompass the variation observed between basal metabolic rates
230 and maximum metabolic rates in empirical studies (Nagy 1987, Gillooly et al. 2001).

231 In total, we simulated 100 webs for each combination of the four foundation species
232 models and the six metabolic treatments: 100 × 4 × 6 = 2,400 food-web simulations. Model code
233 is available from the Harvard Forest Data Archive (http://harvardforest.fas.harvard.edu/data-
234 archive), dataset HF-211.
235
236 ## RESULTS
237 ### *Assembly*
238 #### SPECIES RICHNESS
239 Species richness varied with metabolic rate ($F_{1, 1300} = 224.05$, $P < 0.001$) and foundation
240 species model ($F_{3, 1300} = 13.33$, $P < 0.001$), and there was a significant interaction between the
241 model type and metabolic rate ($F_{3, 1300} = 49.37$, $P < 0.001$) (Fig. 3A). Species richness increased
242 with increasing metabolic rate in the *basal* model webs (slope = 0.082, t = 2.39, P < 0.02),
243 whereas it decreased with increasing metabolic rate in webs derived from the other three models
244 (*total*: slope = –0.51, t = –11.83, P < 0.001; *consumer*: slope = –0.77, t = –16.41, P < 0.001;
245 *control*: slope = –0.29, t = –7.43, P < 0.001). Webs collapsed entirely (i.e., species richness = 0 at
246 $t = 2{,}000$ model time steps) only in the *10*× treatment; these collapses occurred in the *total*
247 (33%), *control* (42%), and *consumer* (2%), but not in the *basal* foundation species models.
248
249 #### FOOD-WEB STRUCTURE
250 The first two principal components of food-web structure (Fig. 4) accounted for 67% of
251 the variation across model food webs (Table 3). Model webs with low PC-1 scores were
252 relatively species-rich with high *C, LS,* and cluster coefficients, and also had a high fraction of
253 intermediate species and omnivores. Conversely, webs with high PC-1 scores were species-poor

254 with low *C* and *LS*; these webs also had long path lengths and large fractions of top, basal, and
255 herbivore species. Webs with high PC-2 scores were species-rich with low *C*, and had large
256 proportions of top species, low proportions of basal species, and low cluster coefficients. Webs
257 with low PC-2 scores were species-poor with high *C* and cluster coefficients, and had a large
258 fraction of basal species.

259 PC-1 scores of food-web structure were significantly associated with model type ($F_{3, 1224}$
260 = 10.78, $P < 0.001$) and the interaction between model type and metabolic rate ($F_{3, 1224} = 15.27$, P
261 < 0.001), but not with metabolic rate alone ($F_{1, 1224} = 1.86$, $P = 0.17$) (Fig. 3B). PC-1 scores
262 decreased with metabolic rate in *basal* model webs (slope = –1.40, t = –3.99, $P < 0.01$), and *total*
263 and *control* webs were not significantly different from the *basal* model webs (*total*: slope = –
264 0.47, t = 1.72, $P = 0.08$, *control*: slope = –1.28, t = 0.2, $P = 0.84$.). In contrast, PC-1 scores
265 increased with metabolic rate in the *consumer* model (slope = 1.55, t = 6.09, $P < 0.001$).

266 Both metabolic rate ($F_{1, 1224} = 23.42$, $P < 0.001$) and model type ($F_{3, 1224} = 6.24$, $P < 0.001$)
267 had significant effects on PC-2 scores, and the interaction term was also significant ($F_{3, 1224} =$
268 7.71, $P < 0.001$) (Fig. 3C). PC-2 scores significantly decreased with metabolic rate in the
269 *control* model webs (slope = -1.45, t = -4.72, $P < 0.001$), whereas the PC-2 scores of the webs
270 generated by the other three foundation species models did not change across metabolic rates
271 (*basal*: slope = –0.02, t = -0.13, $P = 0.90$, *total*: slope = –0.44, t = -1.43, $P = 0.15$, *consumer*:
272 slope = –0.38, t = -1.35, $P = 0.18$).

273

274 *Foundation species removal*

275 SPECIES RICHNESS

Species loss varied across metabolic rate ($F_{1, 1004} = 116.54$, $P < 0.001$) and foundation species model ($F_{3, 1004} = 22.41$, $P < 0.001$) (Fig. 5A). The interaction term (*metabolic rate* treatment × type of *foundation species model*) also was significant (ANCOVA: $F_{3,1004} = 22.27$, $P < 0.001$). Species loss in the *total* (slope = 0.35, t = 8.03, $P < 0.001$), *control*, (slope = 0.11, t = 1.97, $P < 0.05$), and *consumer* models (slope = 0.15, t = 3.34, $P < 0.001$) increased with metabolic rate. The species loss for *basal* model webs was not influenced by metabolic rate (slope = 0.03, t = 1.11, $P = 0.28$). The *10*× treatment was the only treatment in which webs completely collapsed (i.e., had a final species richness of zero) after the removal of the foundation species. Web collapse occurred in the 92 % of the *total* and 40% of the *control* webs.

FOOD-WEB STRUCTURE

The first two principal components accounted for 60% of the variation in food-web structure after the removal of the foundation species (Table 3). Model webs with high PC-1 scores lost a greater proportion of species, and showed relatively larger decreases in *LS* and cluster coefficients (Fig. 6). These structural changes were due primarily to a decrease in the proportion of intermediate and omnivore species and an increase in the proportion of basal species after foundation species removal. Webs with low PC-1 scores lost fewer species and experienced smaller declines or increases in *LS* and cluster coefficients. These webs also had larger proportions of intermediate and omnivore species. Webs with high PC-2 scores lost a greater proportion of species, showed an increase in *C*, and decreased path lengths. Webs with low PC-2 scores lost fewer species, experienced a decrease in *C,* and increased in path length.

Metabolic rate ($F_{1, 974} = 14.36$, $P < 0.001$), foundation species model type ($F_{3, 974} = 21.36$, $P < 0.001$) and their interaction ($F_{3, 974} = 6.61$, $P < 0.001$) significantly influenced PC-1 scores

299 (Fig. 5B). PC-1 scores increased with metabolic rate in webs generated using the *total* (slope =
300 1.35, t = 3.20, $P < 0.01$), *control*, (slope = 1.31, t = 3.31, $P < 0.001$), and *consumer* models
301 (slope = 1.35, t = 3.88, $P < 0.001$). However, PC-1 scores for *basal* model webs were not
302 influenced by metabolic rate (slope = –0.59, t = –1.63, $P = 0.10$). PC-2 scores varied with
303 metabolic rate ($F_{1, 974} = 26.79$, $P < 0.001$), foundation species model ($F_{3, 974} = 5.44$, $P < 0.01$), and
304 their interaction ($F_{3, 974} = 8.59$, $P < 0.001$) (Fig. 5C). PC-2 scores increased with metabolic rate
305 in *basal* (slope = 0.7, t = 2.84, $P <0.01$) and *consumer* (slope = 1.57, t = 2.55, $P < 0.05$) model
306 webs, but decreased with metabolic rate in *total* model webs (slope = –0.14, t = –2.03, $P < 0.05$)
307 and showed no change in *control* webs (slope = –0.03, t = –1.87, $P = 0.06$).
308
309 DISCUSSION
310 Our simulations have illustrated that foundation species can play an important role in the
311 assembly and collapse of food webs. By definition, foundation species influence community
312 composition and functioning largely through non-trophic interactions (Ellison et al. 2005). Here,
313 we have shown that the trophic position of the species that receive benefits (in this case a
314 decrease in metabolic rate) from the presence of a foundation species can influence the food web
315 assembly process and the response of a food web to the loss of a foundation species. When a
316 foundation species lowered the metabolic rate of only basal species the resultant webs were
317 complex and species-rich. In general, *basal* model webs also were robust to foundation species
318 removals, retaining high species richness and complexity. On the other hand, when a foundation
319 species lowered the metabolic rate of only consumer species (our *consumer* model), all species
320 (*total* model), or no species (*control* model) the resultant webs were species-poor and the
321 consumer webs had low complexity (i.e. low *C, LS,* clustering coefficient). Furthermore, the

322 subsequent removal of the foundation species from the *consumer*, *total*, and *control* model webs
323 resulted in a greater loss of species and complexity than in the *basal* model webs.
324 One potential explanation for the species-rich complex food webs produced by *basal*
325 models and the species-poor simplified webs produced by the *consumer* and *total* models may be
326 found in the population dynamics of the system. When a foundation species lowers the metabolic
327 rate of the consumers (top predators and intermediate consumers in both the *consumer* and *total*
328 models), consumer populations reach higher abundances, which in turn can lead to stronger
329 predator-prey interactions (Holling 1965, Abrams and Ginzberg 2000). Strong interactions can
330 lead to unstable predator-prey dynamics and result in the extinction of both the predator and the
331 prey species (May 1972, McCann et al. 1998). In the *basal* model, lower metabolic rates
332 increased energy for growth and reproduction, allowing basal species to withstand transient
333 dynamics of early assembly or low initial population abundances. Once gaining a foothold, even
334 non-foundational basal species can provide multiple energy pathways to species at higher trophic
335 levels. And once the foundation species was removed, the other basal species were already
336 established and maintained energy pathways to higher trophic levels, limiting further extinctions.
337 This mechanism is also consistent with the standard facilitation model of succession (Connell
338 and Slatyer 1977), where later-successional (facilitated) species can maintain high abundances
339 even after early-successional species have disappeared. Two important differences, however, are
340 that in the field, foundation species persist in the system much longer than early-successional
341 species, and associated species composition changes dramatically following foundation species
342 removal (e.g., Orwig et al. 2013).
343 In addition to the trophic position of the target species that a foundation species
344 influences, the magnitude of the metabolic rates of the associated species in the absence of the

345 foundation species (or more generally, the cost of not having the foundation species) was also
346 important in determining food-web structure and the response of food webs to foundation species
347 removal. When metabolic rates were highest in the absences of foundation species (the *10*×
348 treatment), webs lost the most species both during assembly and after removal of the foundation
349 species. The *10*× treatment also was the only one for which webs collapsed entirely (to zero
350 species). This collapse was observed most frequently in the *control* webs, in which the
351 foundation species did not have any non-trophic interactions with other species. Interestingly,
352 *basal* model webs in the *10*× metabolic rate group maintained species richness at levels similar
353 to those seen in the lower metabolic rate treatments. This result is consistent with that seen in the
354 *food-web assembly* dynamics, and implies that facilitation of basal species by foundation species
355 can overcome even the highest metabolic rates (costs). Overall, our results suggest that
356 foundation species that influence other basal species will result in robust food webs, whereas
357 those that influence consumers lead to the loss of species and complexity both during the
358 assembly process and after foundation species removal. Additionally, these effects are magnified
359 when metabolic costs to other species increase in the absence of the foundation species.
360 In our models, foundation species exerted influence by lowering metabolic rates for
361 certain species. This is only one type of non-trophic interaction that can occur in a food web, and
362 it is likely that foundations species have many other non-trophic interactions and effects (e.g.,
363 providing refuge from predators, facilitating establishment; Kéfi et al. 2012) that deserve further
364 exploration. In addition, in all of our models, foundation species had a positive influence on all
365 species at similar trophic positions. In real food webs, however, this generalization is unlikely to
366 hold, as foundation species can have different effects on species that share the same trophic
367 position and may also have negative effects on some species in the food web (e.g., Ellison et al.

2005b, Sackett et al. 2010, Prevey et al. 2010, Kane et al. 2011). Furthermore, the effects of foundation species in our simulations are strongest when associated species do really poorly without the foundation species present (i.e., the *5*× and*10*× metabolic treatments). This result implies that the role of a foundation species largely depends on the magnitude of its influence, but weak trophic (McKann et al. 1998, Neutel et al. 2002, Rooney and McCann 2012) and facilitative links (Allesina and Tang 2012) are also import in maintaining network structure and dynamics. Thus, measuring the influence of foundation species on other species in the food web through experimental removal studies (e.g., Ellison et al. 2010, Sackett et al. 2010) will continue to be an important component of understanding foundation species roles in the assembly and collapse of food webs.

Future exploration of foundation species in both modeled and real food webs should consider how foundations species differentially influence species in similar trophic positions, the threshold of metabolic rates (or other factors that foundations species influence) at which food webs respond, and non-trophic interactions that influence model parameters other than metabolic rate. Nonetheless, this first theoretical exploration of foundation species in a food-web context shows that we should look for foundation species to strongly influence basal species, leading to robust species-rich food webs that are the least susceptible to cascading extinctions when foundation species are lost.

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515 Table 1. Model Variables

Parameter	Description	Value or Equation
M_i	Body mass of species *i*	eq.1
Z	Predator-prey biomass ratio	10^2
T	Trophic level	Calculated using the prey-averaged method
B_i	Biomass of species *i*	Initial draw from Uniform[0.5,1]
r_i	Mass specific growth rate of species *i*	1
K	Carrying capacity	1
G_i	Logistic growth rate of species *i*	1-(*Bi/K*)
x_i	Mass specific metabolic rate of species *i*	0.01
y_i	Maximum consumption rate of species *i*	8
e_{ji}	Assimilation efficiency for species *i* when consuming species *j*	0.85 for carnivores 0.45 for herbivores
f_{ij}	The fraction of species *j* that is ingested by species *i*	1
F_{ij}	Functional response for species *i* feeding on species *j*	eq. 3
w_{ij}	the uniform relative consumption rate of consumer *i* preying on resource	1/number of prey items
B_0	Half-saturation constant	0.5
R	Production	eq. 4a
X	Metabolism	eq. 4b
Y	Maximum consumption rate	eq. 4c
a_r	Allometric constant	1

a_x	Allometric constant	0.314
x_a	Metabolic rate in the absence of the foundation species	Depends on model run; see *exploring parameter space*
x_{fsp}	Metabolic rate of target species in the presence of the foundation species	Depends on model run; see *exploring parameter space*
B_a	Typical biomass for the foundation species	1

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518 Table 2. Metrics of food-web structure

Metric	Definition*
C	connectance, or the proportion of possible links realized. $C = L/S^2$, where L is number of links and S is the number of species
S	species richness
LS	linkage density = L/S, number of links per species
ClustCoef	clustering coefficient, probability that two taxa linked to the same taxon are also linked
PathLen	characteristic path length, the mean shortest set of links (where links are treated as undirected) between species pairs
Top	percentage of top species in a web (taxa have no predators)
Int	percentage of intermediate species in a web (taxa with both predators and prey)
Omniv	percentage of omnivores in a web (taxa that feed on more than one trophic level)
Herbiv	percentage of herbivores in a web (taxa that only prey on basal species)
Basal	percentage of primary producers in a web (taxa that have no prey)

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521 Table 3. Principal component loadings for food-web structure after food-web assembly (t =
522 2,000 modeled time steps) and after foundation species removal (t = 4,000 time steps).
523

Metric	After assembly (t = 2,000)		After foundation species removal (t = 4,000)	
	PC1 (52%)	PC2 (15%)	PC1 (41%)	PC2 (19%)
S	-0.34	0.40	0.36	0.39
LS	-0.40	0.17	0.45	-0.02
C	-0.22	-0.46	0.16	-0.66
Top	0.26	0.32	-0.23	-0.06
Int	-0.40	0.11	0.41	0.15
Basal	0.32	-0.38	-0.39	-0.15
Herbiv	0.28	0.20	-0.17	0.06
Omniv	-0.36	0.19	0.34	0.00
PathLen	0.26	0.31	-0.18	0.59
ClusterCoeff	-0.27	-0.41	0.30	-0.14

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526 Figure Legends

527 Fig. 1. Schematic diagrams of the four foundation species models; A) *control,* B) *basal*,
528 C) *consumer*, D) *total*. White nodes are basal foundation species, gray nodes are other basal
529 species, and black nodes are consumers. Solid black lines with arrows represent trophic
530 interactions and dashed lines are non-trophic interactions (i.e., reduction in metabolic rate).
531
532 Fig. 2. Saturating functions (eqn. 6) relating metabolic rate to foundation species
533 biomass. A) In the absence of a foundation species, species have the baseline, allometrically-
534 scaled metabolic rate (dashed line; eqn. 5b). Increasing the biomass of the foundation species
535 results in an asymptotic decline in metabolic rate to *0.5*× (green), *0.2*× (magenta), or *0.01*×
536 (cyan) the baseline. B) When foundation species biomass = 0, species have metabolic rates *10*×
537 (blue), *5*× (red), or *2*× (orange) the baseline, allometrically-scaled metabolic rate (dashed line).
538 As the biomass of the foundation species increases, metabolic rate declines asymptotically to the
539 baseline. These functions are the six metabolic rate treatments that we applied to the predator-
540 prey model.
541 Fig. 3. ANCOVA plots illustrating species richness (A) and principal axis scores (B, C)
542 of food-web structure after food-web assembly (at t = 2,000 modeled time steps) as a function of
543 metabolic rate and the four types of foundation species models. Green lines and points
544 correspond to the *basal* model, Pink = *consumer* model, Blue = *total* model, and Orange =
545 *control* model.
546
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548 Fig. 4. Principal component biplots of food-web metrics for assembled food webs (at t =
549 2,000 modeled time steps). Illustrations along each PC axis depict representative individual
550 webs.
551 Fig. 5. ANCOVA plots illustrating species richness (A) and principal axis scores (B, C)
552 of food-web structure after foundation species removal (at t = 4,000 modeled time steps) as a
553 function of metabolic rate and the four types of foundation species models. Green lines and
554 points correspond to the *basal* model, Pink = *consumer* model, Blue = *total* model, and Orange =
555 *control* model.
556 Fig. 6. Principal component biplots of standardized change in food-web metrics for food
557 webs after foundation species removal (i.e., $\Delta z = z_{t=2001}\text{-}z_{t=4000} / z_{t=2001}$). Text along each PC axis
558 show general change in food web complexity and richness associated with each axis.
559
560